EFFECTS OF ANTHROPOGENIC FEATURES AND LANDCOVER ON THE LONG-DISTANCE MOVEMENTS OF LESSER PRAIRIE-CHICKENS

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Abstract: Individuals moving among spatially distributed wildlife populations drive large-scale population processes. Due to this, these connective movements can be crucial for population stability. However, in many areas, the ability to make these long-distance movements is being threatened by continued land-use change and fragmentation across the landscape, affecting the permeability of the landscape and making the successful navigation of the matrix more difficult. In order to understand and develop management protocols to preserve movement corridors, we need to study these movements across the landscape. Recent research with lesser prairie-chickens (*Tympanuchus pallidicinctus*) has provided a unique opportunity to study long-distance movements and the landscape features that influence these movements. Using GPS data from across the current distribution of the species, we estimated the response distance to discrete anthropogenic features (i.e., towers and windmills, large and small powerlines, oil wells, roads, and fences) in the landscape on a continuous scale. We also estimated the selection and avoidance of landscape features including landcover types using discrete choice models. We found that lesser prairie-chicken long-distance movements generally indicated an avoidance response to anthropogenic features. While response distance varied among feature types and study regions, birds tended to avoid taller features (i.e., towers and large powerlines) in the landscape at much greater distances than the other features tested. Discrete choice models similarly indicated avoidance to anthropogenic features as well as cropland landcovers. We found that Conservation Reserve Program (U.S. Department of Agriculture Program converting cropland to landcovers supporting conservation) and hay/pasture landcovers were selected for during long-distance movements. These results indicate that minimizing the new construction of anthropogenic features in possible dispersal pathways may be required to maintain matrix permeability, especially for towers, windmills, and large powerlines. Additionally, continued management through the Conservation Reserve Program may create stepping stones through fragmented landscapes. Our results should also be useful for the identification and protection of areas important for connective movements among the lesser prairie-chicken population.

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CHAPTER I

EFFECTS OF ANTHROPOGENIC FEATURES ON LESSER PRAIRIE-CHICKEN (*TYMPANUCHUS PALLIDICINCTUS*) LONG-DISTANCE MOVEMENTS

Abstract

Background: Spatially distributed populations often rely on large-scale processes such as gene flow for long-term population stability. These processes themselves are driven by individuals moving across the landscape through long-distance movements like dispersal. However, as landscapes are continually altered by anthropogenic development, increased fragmentation can impact the permeability of the landscape and threaten the success of these movements. Lesser prairie-chickens (*Tympanuchus pallidicinctus*) have lost significant portions (> 90%) of their historic distribution and are currently a candidate species under the Endangered Species Act. Using a unique dataset of GPS movement locations across their entire geographic distribution, we estimated the response distance to six common anthropogenic features found in their environment (i.e., towers and windmills, large and small powerlines, oil wells, roads, and fences) specifically during long-distance movements. By using cumulative distribution functions to estimate response on a continuous scale, we quantified the spatial scales at which these features may affect movements through connectivity zones.

Results: We found that lesser prairie-chickens generally avoid all anthropogenic feature types we tested despite some variation in the reported response distance among study regions. Lesser prairie-chickens avoided the tallest features (i.e., towers and windmills and large powerlines) at much greater distances in comparison to the other anthropogenic features analyzed.

Conclusions: Our results show that the long-distance movements of lesser prairie-chickens are likely to be affected by behavioral landscape fragmentation through increased development of anthropogenic features in important connectivity zones. As our estimated response distances during long-distance movements varied in comparison to previously reported response distances during other behavioral states (e.g., breeding or nesting), we recommend using long-distance or dispersal specific movement data when asking questions related to connectivity across the landscape.

Background

Both the biotic and abiotic environment affect the distribution and movements of animals across the landscape. Movement allows animals to adjust to changes in their environment (i.e., dispersal, migration; Dingle 1996; Clobert et al. 2001) and use behavioral tradeoffs to maximize fitness (Barten et al. 2001; Zollner and Lima 2005). These processes are complex and occur on multiple spatial and temporal scales, but advancements in our understanding of animal behavior allows a greater comprehension of the system as a whole. Ecological complexity increases as land-use change and fragmentation continue to alter landscapes. While fragmentation is often viewed as the explicit change in patch and landscape metrics such as the edge density or shape complexity of landcover, some features in the environment may cause fragmentation through avoidance behaviors (i.e. avoidance of habitat as a response to a discrete feature) (e.g., FRAGSTATS; McGarial and Marks 1995). Behavioral fragmentation in response to

anthropogenic features has been observed as disruptions to normal behavior such as larger step length when crossing roads (Panzacchi et al. 2013; Kite et al. 2016), limited crossings of powerlines (Pruett et al. 2009), or avoidance of oil well and gas development (Hess and Beck 2012; Northrup et al. 2015).

There are several behavioral strategies that animals may use in response to features in the landscape. Beyer et al. (2016) presents the idea that explicit features in the landscape can impede or disrupt movements of individuals in four different ways. They explain that features can be either barriers (i.e., can be crossed but not circumnavigated), obstacles (i.e., can be circumnavigated but not crossed), impedances (i.e., can be crossed or circumnavigated in a tradeoff of the behavioral cost of circumnavigating vs crossing), or constraints (i.e., can't be crossed or circumnavigated). A feature's exact classification into one of these categories is species specific but may also be context specific to other landscape elements or depend on the behavioral state of the individual, as this state can lead to changes in the response to landscape features (Wilson et al. 2012; Harju et al. 2013; Abrahms et al. 2016). Studying the effects of behavioral-dependent responses to landscape features is the first step to understanding the potential these features have for fragmentation. Long-distance movements (i.e., dispersal, migration, exploratory) are useful in studying population connectivity and corridor conservation when increased fragmentation can disrupt key population-level processes (i.e., gene flow, rescue effect; Hanski 1999; Clobert et al. 2001). A better understanding of long-distance movement behaviors may allow the identification of possible fragmentation sources that could have negative effects on landscape connectivity. Additionally, it may be important to consider specific movement types within this category (i.e. dispersal, migration or exploratory searching), because selection and response to landscape variables could vary during various behavioral states.

Recent research with lesser prairie-chickens (*Tympanuchus pallidicinctus*) has provided a unique data set to study long-distance movements across their distribution (Earl et al. 2016). As a grassland obligate species distributed in the southern Great Plains, USA, the species has

experienced a loss of >90% of their historic distribution (Hagen and Giesen 2005) due mainly to loss of habitat and land use change. The remaining population exists in a highly fragmented landscape that was once contiguous grassland. The species has been listed as a threatened species under the Endangered Species Act but is currently a candidate species due to a federal court ruling that vacated the listing (USFWS 2016). Recent research suggests grouse species respond negatively to anthropogenic features in the environment. These features include windmills, oil and gas wells, power lines, roads, and fences (Walker et al. 2007; Hagen et al. 2011; Jarnevich and Laubhan 2011; Hovick et al. 2014; Winder et al. 2014). However, most of the data has been at the home range scale and immediately around lek locations. Further, the effect of these features during long-distance movements has not been assessed. Lesser prairie-chicken populations are spatially distributed by the locations of their leks (i.e. home ranges usually within 5 km of leks; Taylor and Guthery 1980; Winder et al. 2014). This structure is representative of a spatially structured population, where connectivity can have large effects on the stability of the population, providing further need to study long-distance movements to prevent continued fragmentation in the changing landscape.

Using a dataset from multiple study sites spanning the geographic distribution of lesser prairie-chickens, we aimed to examine behavioral fragmentation through potential impedances or barriers to connectivity. To accomplish this, long-distance movements were used to quantify the spatial scales at which lesser prairie-chickens respond to different anthropogenic features in the environment. We used descriptive feature density analysis and cumulative distribution functions to assess the response of lesser prairie-chicken locations to features compared to random locations across the landscape. We further examined the effects of different feature types, geographic region, and movement types on the response distance. We expected long-distance movements of lesser prairie-chickens to occur at farther distances from anthropogenic features in the landscape than random. In addition, we predicted that the birds would be found at greater distances from taller features in the landscape during these movements and exhibit larger

response distances (i.e., the range of effect) to features that are distributed unevenly within the study areas. We also expected that the distribution and density of some features may vary across regions in the five-state distribution of lesser prairie-chickens, affecting response distances. Differences in movement type (i.e., dispersal, movements between home ranges and exploratory movements) may also affect response distances to anthropogenic features across the landscape. Results from this research will provide estimates of what scales different anthropogenic features within the environment can affect the long-distance movements of lesser prairie-chicken and can be used to ensure connectivity and gene flow among populations.

Methods

Study Area

GPS location data were collected from research projects in southeast Colorado (Cheyenne, Prowers, and Baca Counties), the panhandle of Oklahoma (Beaver County), east-central New Mexico (Chaves, Lea, and Roosevelt Counties), and Kansas including two sites in the south-central region (Clark, Comanche, and Kiowa Counties]) and two sites in northwest Kansas (Gove and Logan County). Due to this, the Kansas study areas were combined into northwest (KS_NW) and south-central (KS_SC) regions to ensure the independence of the data. The New Mexico and Oklahoma study regions included birds with movements that crossed into Texas, and the Colorado study region also had two birds that made long-distance movements in southwest Kansas. There was variation in each of the regions' natural landcover, as they were spread across different ecoregions (McDonald et al. 2014). GPS satellite transmitters were attached to lesser prairie-chickens (n = 346) to collect locations at fixed time points. Similar capture methods were used at each study site and included lek focused dropnets (Silvy et al. 1990) and walk-in drift traps (Haukos et al. 1990; Schroeder and Braun 1993). At capture, gender was determined for each bird based on plumage characteristics (Copelin 1963) and a rump-mounted GPS transmitter (22 g PTT- 100, Microwave Telemetry Inc., Columbia, Maryland,

USA; Model 22GPS, North Star Science and Technology, King George, Virginia, USA) was attached. Captures occurred from March 2013 through April 2016, and data was collected through December 2016.

Movement Classifications

Using the GPS locations received from these projects, long-distance movements were delineated for each individual. Similar to Earl et al. (2016), any consecutive groups of points (i.e., bursts) found greater than 5 km net displacement outside of the observed home range was considered a long-distance movement. Home ranges were defined using kernel utilization density-based home range analysis (Worton 1989) with the R package "adehabitathr" (Calenge 2006). These movements were then separated into three categories. First, if an individual made a long-distance movement that went between two separate home range polygons, the movement was considered a home range to home range movement, hereafter "HR to HR." These were representative of both dispersal movements, where an individual moved from an established home range and into a new area at least 5 km away and established a new home range, and round-trip movements (e.g., partial migration or seasonal movements) between two established home ranges. Separating between these two types of movements is difficult without location data for the entire lifespan of the individuals because it is unclear if an individual had used a home range previously before capture or if it was a true dispersal event. Due to this difficulty, these movements were grouped into one category for our analysis. The second movement classification occurred when a movement left a home range polygon, ventured at least 5 km net displacement away, and returned to the same home range polygon. These movements were classified as "Foray Loops" and were representative of search strategies and long-distance movements that did not end in reaching or establishing a different home range area. The final category consisted of the movements that could not be determined to fit the other categories for one of two reasons: either the movement began at the capture of the individual or ended with the individual's death or the

permanent malfunction of its satellite transmitter. In either of these cases, only one end of the movement was bounded by a home range polygon, while the beginning or end of the movement was unbounded from an established area of use. These "Unclassified" movements are not distinguishable as one of the other movement types but still contain information on how individuals use the environment during long-distance movements and were included in the analysis.

Feature Description

We examined the effects of roads, power lines, oil wells, tall towers, and fences on lesser prairie-chickens. Road data was downloaded from the U.S. Census Bureau 2016 TIGER/Line dataset for the entire distribution. This included both higher traffic, paved roads and rural road networks in our study area. We initially wanted to separate road features into categories of average traffic use, as lesser prairie-chicken response to these features likely varies for this metric. However, we were unable to obtain traffic data for all roads in such a large study area, so all were analyzed together for our study. We were able to split powerline data into two categories by size for analysis purposes due to a difference in potential response. Large power lines were defined as powerlines greater than 69kV and were obtained from the U.S. Department of Homeland Security for the entire geographic distribution. These features were much taller and more visible from farther distances in comparison to the smaller powerlines used for local energy distribution. Small powerlines were those that are less than 69kV, and data was gathered from the Southern Great Plains Crucial Habitat Assessment Tool (Klute et al. 2013). This dataset was incomplete for most of the study areas and could only be used for analysis in the Oklahoma region. For the oil well category, we used active oil and gas well locations identified between 2010 to 2013 from the Southern Great Plains Crucial Habitat Assessment Tool (Klute et al. 2013). This dataset was incomplete in the Colorado study region. While inactive wells could also impact movements, we couldn't find reliable data across our entire study region detailing when

pumps were active vs inactive, so we used this dataset for consistency. The tall tower dataset included any structure larger than 50 ft (i.e., poles, towers, buildings, windmills, stacks, utilities) and was obtained from the Federal Aviation Administration's Digital Obstacle File for the entire study area. Finally, fence data was collected at five of the original study sites and digitized into shapefiles using ESRI ArcGIS 10.3 (ESRI 2014). This data only included parts of the Oklahoma and parts of both Kansas study regions. This mapping was focused around the home ranges of individuals and capture locations and did not cover all long-distance movement tracts in these covered areas.

Statistical Analysis

First, we calculated feature density estimates across the different study regions and movement types. To do this, all long-distance movement lines were buffered by 25 km. This distance was chosen to provide a broad estimate of the area avaiable to lesser prairie-chickens during long-distance movements. Dissolving these buffers together, we divided the polygon into 2 km^2 indexed grid polygons and clipped each feature type to every grid cell to obtain the density of features across the landscape. The individual buffers were then dissolved by both the study regions (i.e. Oklahoma, Colorado, Northwest Kansas, Southcentral Kansas, and New Mexico) and movement types (i.e. HR to HR, Foray Loop, and Unclassified) separately and mean density and standard error was calculated for each of the resulting polygons to assess differences. This was conducted using a combination of ESRI ArcGIS and R (*version 3.4.2*, R Core Team 2017).

We then used cumulative distribution functions (CDFs) to determine the selection/avoidance/neutral responses of lesser prairie-chickens as a function of distance to each feature type. The difference of the cumulative density of used points and random points in the study area were used to estimate the selection of a resource compared to random. This method creates a function where positive, negative, and relatively flat (nearing 0) slopes indicate selection, avoidance, and neutral behaviors respectively, in relation to a continuous variable.

CDF-based selection models have been implemented with slightly different methodologies (Kopp et al. 1998; Dunkin et al. 2009; Martin and Shepherdson 2012; Tanner et al. 2015) depending on whether the study species locations or the features were randomized across the landscape. Because we had both point and linear vector features, we replicated the lesser prairie-chicken locations. The difference in the cumulative frequency of the observed data (G[x]) and the random, pseudo-relocations (F[x]) as functions of distance to the nearest feature allows a selection/avoidance/neutral trend line to indicate the response to a feature on a continuous scale (Dunkin et al. 2009).

To obtain the pseudo-location CDF, thirty random points were drawn from the study area for each lesser prairie-chicken location to create a list of available pseudo-locations. For this list, the distance to the nearest feature was estimated. Over 30 iterations, points were randomly selected from the available location list to include in each iterations' CDF with bins set every 50 m (Dunkin et al. 2009; Tanner et al. 2015). For each iteration, the number of points randomly selected was equal to the number of actual lesser prairie-chicken locations in the study area. The final mean pseudo-relocation CDF (F[x]) and standard error were calculated using CDFs from each iteration. G[x] was calculated by organizing the cumulative frequency of the nearest distance between actual relocations and features in the study area by the same distance bins. The function G[x] – F[x] results in the response curve, where positive slope indicates that the actual lesser prairie-chicken relocations (G[x]) accumulate faster in relation to distance to nearest feature than the random pseudo-relocations (F[x]) specifying selection or attraction at that distance while negative slope represents the opposite indicating avoidance behavior at that distance from the nearest feature. Because cumulative density distributions always add up to 1, causing the selection/avoidance/neutral trend to always return to zero eventually, generally only the initial response trend at the shortest distances have biological relevance.

The above method for determining the CDF selection curve was used to assess the response to anthropogenic feature classes among regions, movement types, and when all the data

was analyzed together. However, the scale at which lesser prairie-chickens perceive features in their environment and respond to them during long-distance movements was unknown, and the scale for response is most likely different during long-distance movements compared to movements within home ranges (Harju et al. 2013). To address this, the long distance movement tracts were buffered by different distances to create the available area that the random relocations were selected from. We tested 20 different availability scales with buffer distances ranging 1 km up to 20 km in 1 km increments. This was chosen to cover all possible scales of selection up to at least the average net displacement of long-distance movements of lesser prairie-chickens at 16 km (Earl et al. 2016). All CDF analyses were conducted in R.

Results

We examined location data for 346 lesser prairie-chickens. Of these, 85 made movements greater than 5 km from their home range that were included in the analysis. This totaled 4,757 locations, which was less than one percent of the entire dataset. There were 184 separate long-distance movement tracts (Table 1). The Kansas study regions had the most birds with long-distance movements, while New Mexico had the least. New Mexico only had birds that made HR to HR movements. The most common movement type was HR to HR (74.4%) followed by Foray Loops (19%). At least four birds from each study area made more than one long-distance movement totaling 39 birds. Of these, 13 birds made movements of different types, with at least one from every study area except for New Mexico (Table 1).

Feature Density

Feature density varied across all regions (Table 2). Oklahoma had the highest density for every feature type. Road density was significantly different among all regions with Colorado having almost 1 km fewer roads in each 2 km^2 grid cell on average. Small powerline density was only calculated in the Oklahoma study region, as we lacked complete data in the other regions.

The second highest density of oil wells was found in New Mexico, but the estimate was similar to the Kansas south-central study region. The Oklahoma study region had the highest density of fences, averaging over 8 km of fence line in each 2 km^2 grid cell. In contrast, the two Kansas regions were similar and averaged almost 3 km of fence lower than Oklahoma. Both large powerline and tower features had similar estimates among study regions. For each of these features, the lowest density was found in New Mexico, and Oklahoma had the highest density.

There was less variation when comparing feature density among movement types (Table 2). The densities of both small powerlines and fences were not significantly different among movement types. Large powerline and tower densities estimates were similar in that the areas with "Unclassified" movements had significantly higher densities than the areas with "Foray Loops" or "HR to HR" movements. Road density varied significantly among all movement types. The highest road density was found in areas with "Unclassified" movements, while the areas surrounding "Foray Loops" had the lowest road density. Areas containing "Foray Loop" movements had higher oil well densities than the other movement types.

Cumulative Distribution Functions

The most common selection/avoidance/neutral trend was for lesser prairie-chickens to avoid features at the nearest distances. The reported response distance is where the trend then begins to neutralize after an initial inflection as the distances increase from the feature. However, this was not seen in all regions, movement types, or study area buffer sizes. We found similar response distances among movement types (Table 3). As the responses for movement types were also similar to the results when all the data was analyzed together, we decided to focus the rest of our analysis and conclusions on the CDF results among regions and the full dataset. However, the full CDF results for movement types can be found in the supplemental data (Appendix A) as well as the reported response distances (Table 3). In addition, we found that there was little variation in the estimated response distance as the available area buffer changed, especially after 5 km. Due

to this, we reported the average of the CDFs across all buffer sizes to simplify the results from our analyses but included the full results in supplementary data (Appendix B).

To ensure that there wasn't spatial correlation between the different anthropogenic features, particularly small powerlines, roads, and fences as these three features are often found near each other, we used the grid cells from the feature density part of our analysis to test the correlation between the total distance of these features. We found that there was some correlation between small powerlines and roads in Oklahoma with a correlation level at 0.63, but all other correlation estimates were < 0.25. For all CDF analyses of small powerlines, only the Oklahoma data was used resulting in the same graph and response distance for the Oklahoma region and the full dataset (Table 3; Figure 1). Lesser prairie-chickens avoided small powerlines up to 350 m, where the graph inflected and began to neutralize. Road CDF results indicated avoidance at the closest distances across all analyses (Figure 1). However, there was some variation in response distance, with the lowest response estimate in the Kansas Southcentral region and the highest in the Kansas Northwest (150 and 700 m respectively), with the others intermediate (Table 3). We only had fence data for certain parts of the Oklahoma and Kansas regions. Fence estimates varied between all regions with both Kansas regions and the full dataset CDFs indicating avoidance at the closest distances with a maximum response of 400 m, while in Oklahoma we observed selection for fences at the closest distances (Figure 1). This selection response for fences in Oklahoma inflected after the first distance lag (i.e., 50 m) and began to neutralize. For oil wells, we were missing data for the Colorado region but found similar avoidance response distance among the Kansas and Oklahoma regions, as well as the full dataset at between 350 and 400 m (Table 3). However, the estimated avoidance response distance in New Mexico was 2.25 km.

The taller features in the landscape (i.e., large powerlines and towers) generally had larger estimated avoidance response distances in comparison to the other feature types but also had large regional variation (Figure 1). For large powerline CDFs, the Colorado region had the largest estimated response distance followed by New Mexico and Kansas Northwest (> 9 km;

Table 3). The Kansas Southcentral region and the full dataset estimates were intermediate at 6.00 and 5.65 km respectively and in Oklahoma the estimate was much lower at 2.95 km. Tower CDFs for the full dataset had the highest response distance estimate at 9.25 km followed by NM and the Kansas regions. The Colorado region's response was lower at 2.70 km, but Oklahoma was the lowest at 900 m.

Discussion

This study is the first to provide quantitatively derived estimates of response to anthropogenic features during long-distance movements for lesser prairie-chickens, as well the first of its kind to provide these estimates using data from across the entire distribution of a species. We found that lesser prairie-chickens generally exhibit avoidance to all feature types we examined with some variation in the response distance among regions. Our study adds further justification that anthropogenic features have the potential to disrupt movements of wildlife species (e.g., Polfus et al. 2011; Laberee et al. 2014). Because long-distance movements are an individual-based behavior that can have consequences on population-level dynamics (Hanski 1999; Clobert et al. 2001), these movements play a crucial role in the persistence of spatially structured populations, and our understanding of them allows us to better manage connectivity across the landscape.

Our estimated response distance varied in comparison to other grouse studies with tower and large powerline CDF analyses indicating much greater response distances, while roads and oil wells resulted in smaller estimated responses than the previous studies (Holloran and Anderson 2005; Pitman et al. 2005; Walker et al. 2007; Hagen et al. 2011; Winder et al. 2014). This could indicate differences in response during different behavioral states or periods in the life cycle of grouse, as most of those studies focused on lek persistence, general home range movements, breeding season movements, or nest site selection. As these separate behaviors occur at different temporal and spatial scales, it may suggest that there is variability in how individuals

use their perceptual range to make context or behavior specific decisions (Olden et al. 2004; Pe'er and Kramer-Schadt 2008).

As we predicted, response distances were greatest when examining the tallest features in the landscape (i.e. tower and large powerline features). A similar avoidance response to wind farms has been reported in other bird species (de Lucas et al. 2007; Pearce-Higgins et al. 2009). However, a recent review points out the difficulty in isolating response to these features from other potential casual factors such as habitat structure, predation pressure, or confounding factors from other sources of anthropogenic disturbance (Walters et al. 2014). Despite this, lesser prairie-chickens can likely perceive taller features from farther away and thus may be more likely to avoid them for greater distances than shorter features because vertical features may be an indicator of lesser quality habitat in grasslands (Pruett et al. 2009; Hagen et al. 2011).

Our measured response distances are likely relative estimates as any number of environmental cues may be used by an individual to make navigation decisions (Goodenough et al. 2009; Yahner 2011). This leads to a gradient in the effect these features may have on movement and permeability of the landscape (i.e., the point a feature moves from being a barrier, obstacle, or impedance to a constraint; Beyer et al. 2016). However, we need empirical estimates of response similar to those obtained in this study to develop management protocols so connectivity can be preserved before fragmentation reaches a point of no return (Fuhlendorf et al. 2017). This study provides estimates that allow an initial understanding of how anthropogenic features can affect the functional heterogeneity of the landscape during long-distance movements of lesser prairie-chickens (Li and Reynolds 1995). As discrete landscape features such as anthropogenic structures may induce an avoidance response to habitat causing landscape fragmentation, there is a need for more studies that focus on understanding the possible impacts these features have on connective movements.

Habituation is a behavioral and physiological process that results in a decreased responsiveness to stimuli after repeated encounters (Blumstein 2016). This process has been used

to describe a reduced avoidance response of wildlife to anthropogenic features in the environment (Madsen and Boertmann 2008; Johnson and Russell 2014). In our study, we found some support for this idea in regions with the highest densities of anthropogenic features distances having some of the lowest response distances (e.g., towers in the Oklahoma study region; Figure 1). In addition, the only feature examined that had a selective response at the closest distances was fences in Oklahoma, where the fence density was significantly higher than the Kansas regions (Table 2). Despite some support for the process of habituation and tolerance to landscape features, the topic is still debated (Beale 2007; Bejder et al. 2009). This relationship could also be related to the structure of features across the landscape. If the increased fence density in the Oklahoma region correlates with more fences built in the interior portion of the generally grid-like road and small powerline distribution common across our study area, this apparent observed selection to fences could be related to a stronger behavior to avoid those other features.

We also found that there was more variation in the response distances among regions for each feature type than when compared among movement types (Table 3). Response to features during different movements was similar to our full population estimates (Table 3). Exploratory movements such as foray loops are commonly attributed to dispersing individuals. These movements are likely used to better inform their directional decisions and balance the costs associated with leaving their home range (Conradt and Roper 2006). However, dispersers do not seem to follow this pattern in lesser prairie-chickens (Earl et al. 2016). The similarities in the estimated response distances between the movement types may indicate that the observed exploratory loops are abandoned dispersals, where the individual decided to return to their established home range (Conradt et al. 2001).

In our analysis, we thought it would be important to consider the range of values and how CDF response distances change when varying the size of available area because this is the scale of selection during long-distance movements and has not been studied previously (Appendix B). For most CDF combinations of region, movement type, or the full dataset, even if there was

variance in line position on the y-axis, the distance from feature varied only slightly for the inflection points that describe the response distance. The outlying trends were only seen at scales less than 5 km and were likely affected by misrepresented distributions of features. In other words, at these small scales, there may have only been very few features included in the analysis skewing the distance to nearest feature estimates. Essentially, the average of the CDFs across all buffer sizes was sufficient to draw conclusions from and were used to present our results (Figures 1; Appendix A).

Cumulative distribution functions provide a way to measure responses on a continuous scale (Kopp et al. 1998). It is important to note that this method does not allow the estimation of magnitude of effect. While the magnitude of these effects during long-distance movements still needs to be assessed, this study provides evidence that birds do respond to anthropogenic features in the landscape when making long-distance movements. Additionally, it is also important to consider that this method only accounts for distance to nearest feature. Other physical features of these structures, including density, height, or the amount of sound or light produced by them, may influence how lesser prairie-chickens respond to anthropogenic features. The x-axis in CDF analysis can be adapted to different continuous metrics (i.e. density or time since fire; Martin et al. 2012). Ultimately, we were interested in obtaining an estimate for the direction and scale of the response to anthropogenic features during long-distance movements and CDF analysis by nearest distance allowed this. However, there are many other relevant movement and resource selection related questions remaining, such as how does response to features impact fitness or overall permeability of the landscape.

Conclusions

With the southern Great Plains already experiencing large amounts of habitat loss and fragmentation, it is imperative that consider management for lesser prairie-chickens at the landscape scale to ensure continued population persistence (Fuhlendorf et al. 2017). We found

that lesser prairie-chickens locations during long-distance movements were found farther than expected by random chance to almost every anthropogenic feature we tested. This response coincides with past research on the effects of these features on grouse species and provides further evidence they can have a negative effect at all life stages and behavioral states (Hovick et al. 2014). In particular, the tallest features we tested (i.e., large powerlines and towers) tended to have the largest response distance estimates, usually several kilometers. The estimated response distance to these features from previous studies has often been greater than 1.4 km despite the behavioral state of the individual (e.g., nesting, normal movements, lekking; Pitman et al. 2005; Pruett et al. 2009; Hagen et al. 2011), but our estimated response distance for long-distance movements was typically much greater. This could indicate that these tall features are the most important to manage for in order to preserve connectivity in this species as they are likely to have the widest range of effect on impeding these movements across the landscape. Data from this study will help parameterize these models to define the important areas across the distribution of the lesser prairie-chickens to maintain connectivity within the metapopulation and prevent further fragmentation of these important grassland ecosystems.

Long-distance movements are the mechanism behind gene flow and recolonization in a metapopulation system (Hanski 1999; Clobert et al. 2001). Dispersal and migration movements are needed for population persistence in spatially distributed species (Tromeur et al. 2016), but studying these large-scale movements is often difficult and not feasible in individual studies due to the rarity of capturing a significant sample of these events. There is potential in a variety of species for researchers to collaborate, making large-scale studies such as this one more feasible. Without collaboration, this study would not have been possible. Combining data from multiple study areas collected during the same time allowed us to estimate responses to anthropogenic features in the landscape and demonstrate their potential to disrupt long-distance movements in an already fragmented landscape. The results from this study provide a starting point to ensure metapopulation connectivity for lesser prairie chickens, but more information is needed

concerning the magnitude of these effects, the impacts of other physical features of anthropogenic structures, and how these features affect fitness in order to fully inform connectivity models for this species.

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Table 1

Counts of lesser prairie-chicken long-distance movements by movement type (columns) and study region (rows) including summary information for the number of birds making these movements.

Region	HR to HR[1]	Foray Loop	Unclassified	Total	# LPC	# LPC with Multiple Long-Distance Movements	# LPC with Movements of Different Types
Colorado	28	6	0	34	9	6	1
Kansas	25	9	5	39	25	10	2
Northwest Kansas	42	13	5	60	33	11	8
Southcentral New Mexico	21	0	0	21	5	4	0
Oklahoma	21	7	2	30	13	8	2
Total	137	35	12	184	85	39	13
# LPC	57	29	12	-	-	-	-

[1] Home range to home range movements

Table 2

Density of anthropogenic features in study regions and movement types in 2 km^2 grid squares [mean ± SE]

Region/ Movement Type	Fence Distance (m)	Oil Well Count	Large Powerline Distance (m)	Small Powerline Distance (m)	Road Distance (m)	Tower Count
CO	- [1]	-	93.56 ± 6.76$^{A, B}$	-	3174.62 ± 50.14^{A}	0.03 ± 0.01^{A}
KS NW	5477.19 ± 189.33^{A}	0.54 ± 0.02^{A}	146.77 ± 9.38^{C}	-	4055.37 ± 58.3^{B}	0.06 ± 0.01$^{A, B}$
KS SC	5396.05 ± 188.26^{A}	0.88 ± 0.03^{B}	128.76 ± 9.28$^{A, C}$	-	4396.97 ± 58.98^{C}	0.11 ± 0.02$^{B, C}$
NM	-	1.01 ± 0.06^{B}	81.92 ± 7.7^{B}	-	4720.83 ± 67.01^{D}	0.02 ± 0^{A}
OK	8166.5 ± 695.65^{B}	1.92 ± 0.04^{C}	218.49 ± 17.89^{D}	2943.5 ± 66.33^{A}	5626.46 ± 73.95^{E}	0.16 ± 0.02^{C}
Foray Loop	5738.8 ± 142.91^{F}	1.2 ± 0.03^{F}	141.87 ± 7.19^{F}	3147.86 ± 76.65^{F}	4135.97 ± 37.51^{F}	0.07 ± 0.01^{F}
HR to HR	5678.4 ± 138.91^{F}	1.06 ± 0.02^{G}	135.04 ± 5.37^{F}	3104.83 ± 74.42 ^{F}	4521.26 ± 31.89^{G}	0.07 ± 0.01^{F}
Unclassified	5904.39 ± 153.86^{F}	1.07 ± 0.02^{G}	220.22 ± 10.91^{G}	3351.58 ± 88.57^{F}	4805.51 ± 51.39^{H}	0.13 ± 0.01^{G}

[1] Dashes indicate areas removed from analysis due to missing feature vectors in the study area.

[A-E] Regions with different letters within a column indicate significant differences (95% CI) in feature density.

[F-H] Movement types with different letters within a column indicate significant differences (95% CI) in feature density.

Table 3

Summary of response distances (in meters) of lesser prairie-chickens for each feature type identified through the CDF analysis. All distances represent avoidance behaviors unless otherwise reported.

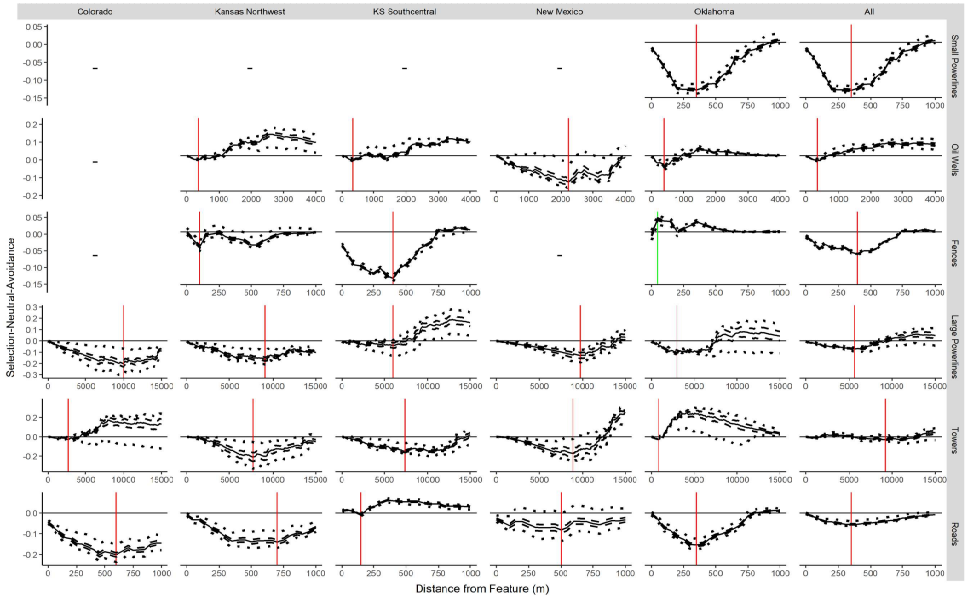
Region/ Movement Type	Fences	Oil Wells	Large Powerlines	Small Powerlines	Roads	Tower
CO	-[1]	-	9950	-	600	2700
KS NW	100	350	9100	-	700	7700
KS SC	400	350	6000	-	150	7350
NM	-	2250	9750	-	500	8900
OK	+50[2]	400	2950	350	350	900
All	400	350	5650	350	350	9250
Foray Loop	400	350	5950	200	450	11250
HR to HR	400	350	5650	250	350	9250
Unclassified	400	400	5500	400	300	7850

[1] Dashes indicate areas removed from analysis due to missing feature vectors in the study area.

[2] The plus sign indicates a selection preference to the indicated distance.

Figure 1

Selection-neutral-avoidance summary outputs from CDF analysis by study region, the full movement dataset, and feature type. Each graph displays the mean selection-avoidance-neutral response line (solid) from the 20 available area buffers, along with 95% confidence intervals (dashed), and range (dotted). Vertical line indicates the response distance (i.e., inflection point), with color representing if the initial response was avoidance (red) or selection (green). Positive slope indicates selection, negative slope indicates avoidance, and neutral slope indicates no preference. Dashes depicts regions and feature type combinations that the feature dataset was incomplete for and not included in analysis.



Appendix A

Figure A1

Selection-neutral-avoidance summary outputs from CDF analysis by movement and feature type. Each graph displays the mean selection-avoidance-neutral response line (solid) from the 20 available area buffers, along with 95% confidence intervals (dashed), and range (dotted). Vertical line indicates the response distance (i.e., inflection point), with color representing if the initial response was avoidance (red) or selection (green). Positive slope indicates selection, negative slope indicates avoidance, and neutral slope indicates no preference.

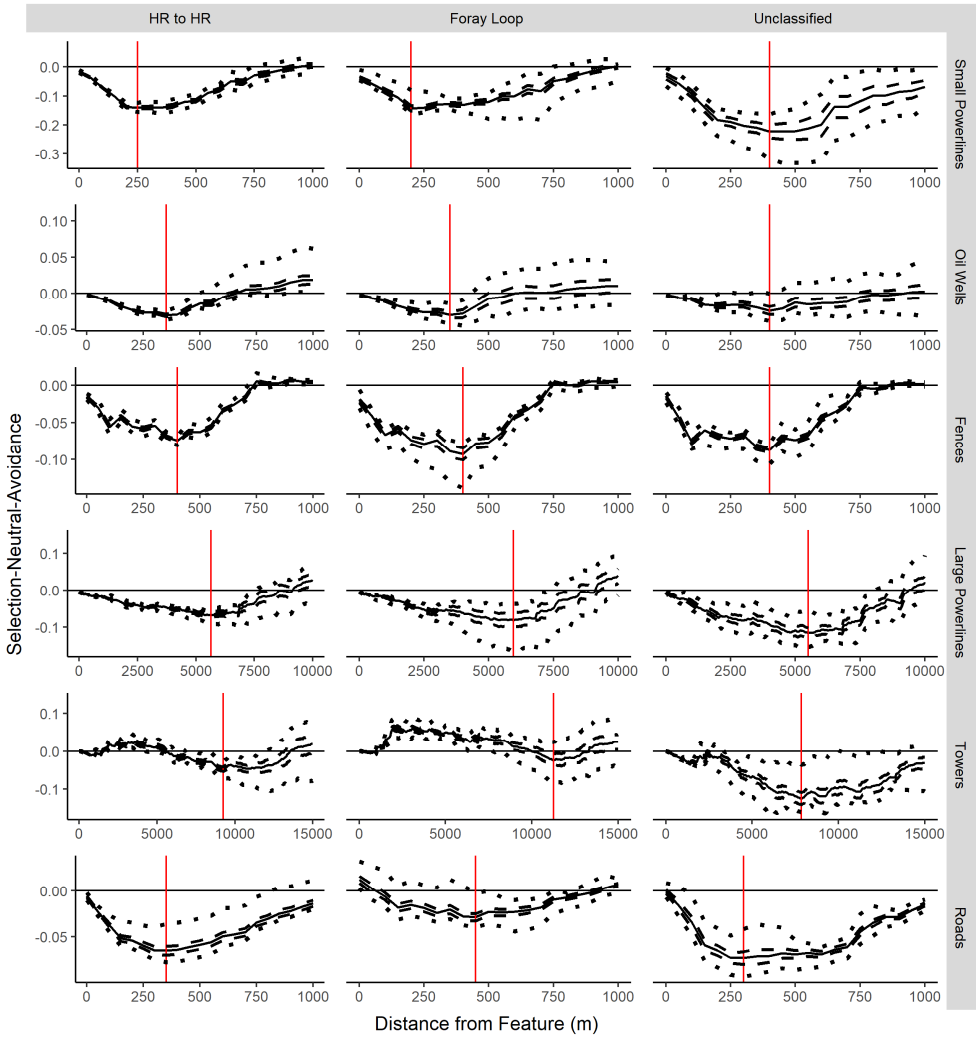


Figure B1

Selection-neutral-avoidance outputs from CDF analysis by study region and feature type. Each line depicts the size of the available area for analysis from 1000 m buffer of long-distance movements to 20000 m (light gray to black respectively). Vertical line indicates the response distance (i.e., inflection point), with color representing if the initial response was avoidance (red) or selection (green). Dashes depicts region and feature type combinations that the feature dataset was incomplete for and not included in analysis.

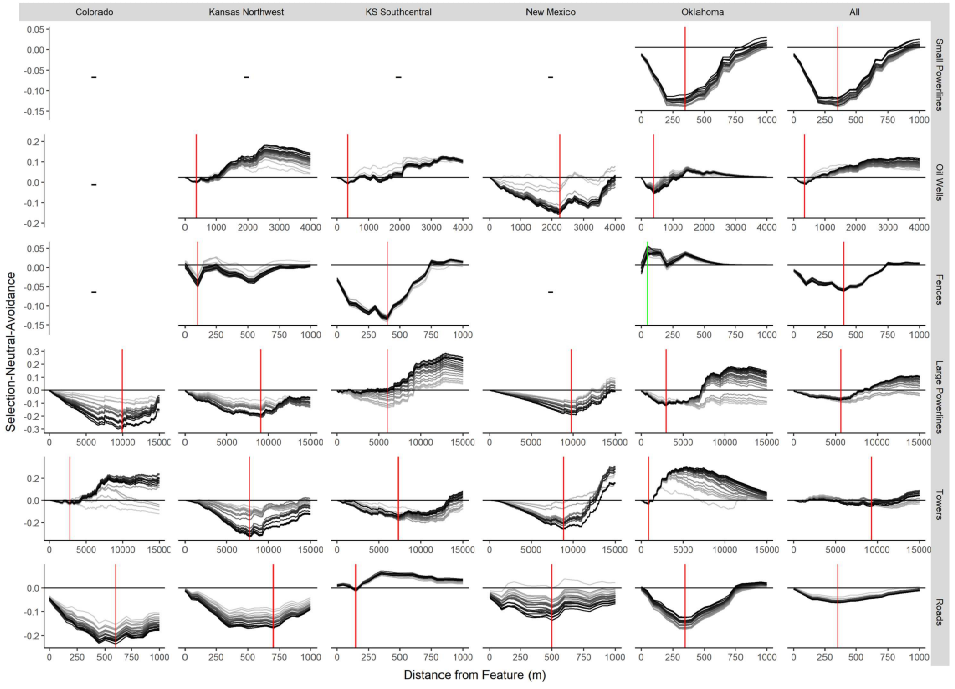
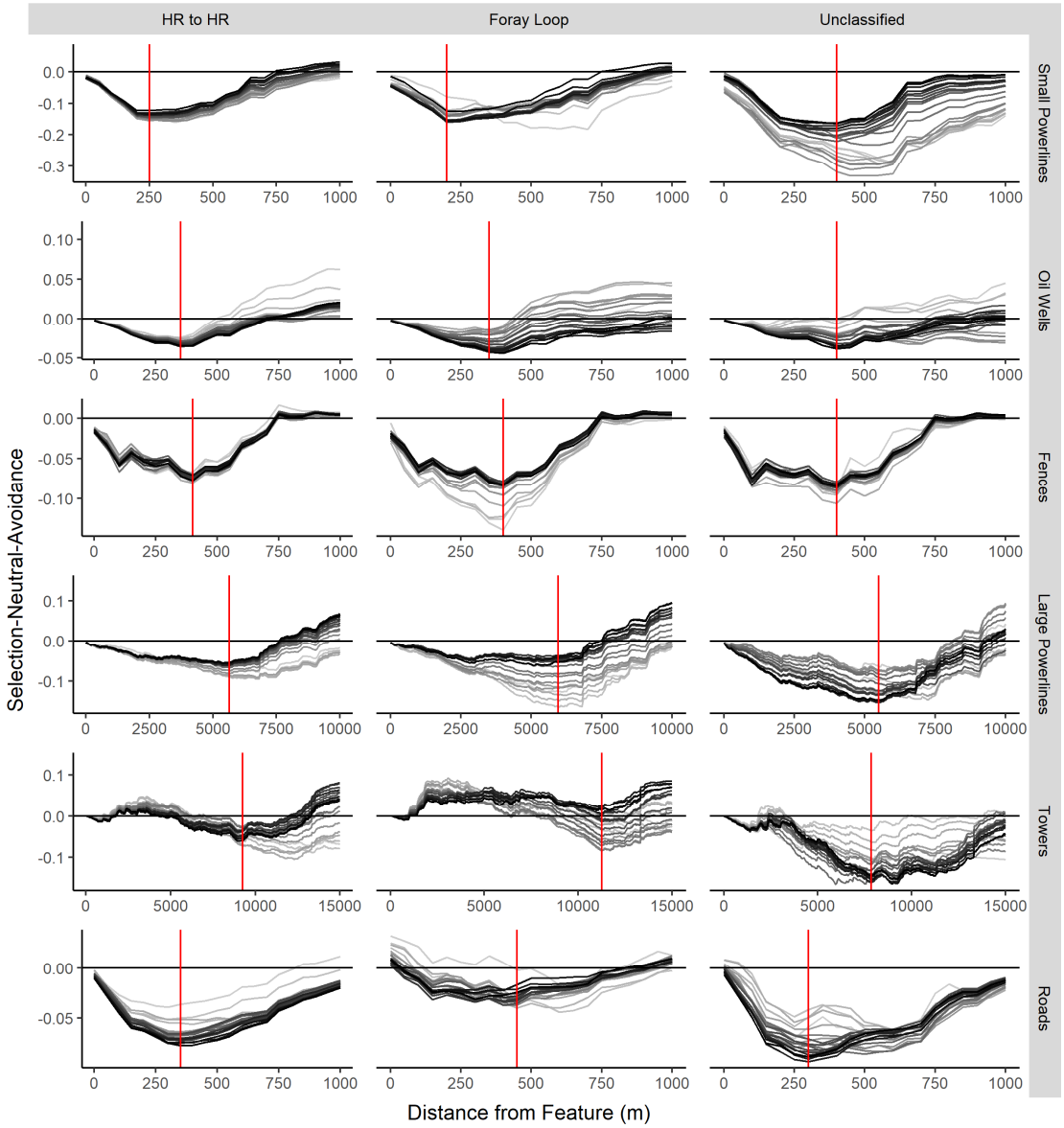


Figure B2

Selection-neutral-avoidance outputs from CDF analysis by movement and feature type. The last column shows the results for all features across every region and movement type assessed together. Each line depicts the size of the available area for analysis from 1000 m buffer of long-distance movements to 20000 m (light gray to black respectively). Vertical line indicates the response distance (i.e., inflection point), with color representing if the initial response was avoidance (red) or selection (green).



CHAPTER II

ENVIRONMENTAL AND ANTHROPOGENIC LANDSCAPE EFFECTS ON RESOURCE USE DURING LONG-DISTANCE MOVEMENTS OF LESSER PRAIRIE-CHICKENS (TYMPANUCHUS PALLIDICINCTUS)

Abstract

Connectivity across the landscape can be crucial for population stability in spatially distributed populations. Large-scale population processes, such as the rescue of sink populations and gene flow, are driven by individuals making long-distance movements across the landscape. However, increasing rates of land-use change and anthropogenic development across many landscapes worldwide threatens the ability for individuals to move across the landscape. Understanding the parameters or landscape features that are selected for or avoided during long-distance movements should help establish conservation guidelines to help protect the integrity of connective pathways through corridor management. Using a unique dataset compromising GPS movement data from across the entire current distribution of lesser prairie-chickens (*Tympanuchus pallidicinctus*), we assessed the selection of landcover, multiple anthropogenic features (i.e., oil wells, roads, towers, large powerlines, and fences), and elevation during long-distance movements using discrete choice models. With a two-step model selection process, we first identified the best metric for selection using univariate models for each anthropogenic feature and then applied the selected metrics to alternative models of selection. We found that

lesser prairie-chickens preferentially use Conservation Reserve Program (U.S. Department of Agriculture Program converting cropland to landcovers supporting conservation; CRP) and hay/pasture landcovers during these movements while avoiding cropland. Additionally, lesser prairie-chickens responded negatively to all anthropogenic features we tested. Our results indicate that continued CRP management to create stepping stones through heavily altered landscapes may help maintain connectivity between populations. We recommend minimizing the construction of new anthropogenic features around possible dispersal routes. These results should assist in the identification and protection of areas critical for connective movements across the lesser prairie-chicken population.

Introduction

Connectivity describes an individual's ability to disperse between habitat patches allowing the rescue of sink populations (Hanski 1999), maintain gene flow (Clobert et al. 2001; Hedrick 2011), and adjust to changes in the landscape (e.g., habitat loss, fragmentation; Fischer & Lindenmayer 2007), or climate (Heller & Zavaleta 2009). However, the degree of connectivity is threatened in many human-dominated landscapes worldwide (Bennett 2003). In spatially structured populations such as metapopulations, corridor conservation can ameliorate the effects of habitat loss and fragmentation on population persistence (Beier & Noss 1998). Corridor-focused management works to maintain population connectivity through the protection of existing linkages or through the restoration of altered landscapes (Bennett 2003; Donald & Evans 2006).

Connectivity between populations is driven by long-distance movements (e.g., dispersal, migration, or exploratory movements outside home ranges). Understanding how these movements are affected by features in the landscape is crucial in the development of conservation corridors. It is understood that animal movement is influenced by an individual's behavioral state and can lead

to differences in resource selection (Wilson et al. 2012; Harju et al. 2013; Abrahms et al. 2016a). However, dispersal events are often not examined explicitly in the creation of conservation corridors and may lead to improperly informed corridor placement (Abrahms et al. 2016b; Blazquez-Cabrera et al. 2016). While a variety of internal and external cues can impact an individual's movement decisions, corridor management generally focuses on landscape features such as landcover or discrete structures that may impede connectivity (Festa-Bianchet & Apollonio 2003; Fischer & Lindenmayer 2007). Understanding how dispersal movements are affected by features in the landscape is crucial in the development of conservation corridors.

Lesser prairie-chickens (*Tympanuchus pallidicinctus*) are a species that can serve as an indicator of broad-scale fragmentation and local conditions in grasslands of the southern Great Plains of the United States. With populations monitored closely due to their decline in distribution and density, they have been in the spotlight for grassland conservation and are currently under review for the Endangered Species Act. Lesser prairie-chickens currently inhabit only about 10% of their historic distribution (Hagen & Giesen 2005). Much of this decline has been attributed to land use change and continued fragmentation of native grasslands across the landscape. The main source of habitat loss has been due to the conversion of grassland to row-crop agriculture but has been further influenced by the encroachment of trees into remaining grasslands (Fuhlendorf et al. 2017). There has been an effort to minimize these effects and restore grassland connectivity through the implementation of the Conservation Reserve Program (CRP; Tanner & Fuhlendorf 2018), a U.S. Department of Agriculture program that provides incentives to landowners that remove cropland from the production cycle and manage it for soil, water, and wildlife conservation. In addition to direct loss of habitat, research indicates that grouse species may be displaced by the presence of anthropogenic features (e.g., oil and gas wells, powerlines, windmills, towers, fences, buildings, roadways; Walker et al. 2007; Pruett et al. 2009; Hagen et al. 2011; Robinson et al. 2016; Harrison et al. 2017) during all periods of their life cycle (Hovick

et al. 2014). However, the direct effects of landcover or anthropogenic features have not been examined during the long-distance movements that directly relate to population connectivity.

Using movement data of lesser prairie-chickens from across their current distribution, our goal was to estimate the selection of landcover types and the magnitude at which anthropogenic features in the landscape may influence long-distance movements. For landcover, aside from general use patterns of cover types common in the southern Great Plains, we were specifically interested in the use of CRP land during long-distance movements, as this could be an important management tool to provide a stepping-stone in the fragmented grassland landscape. In addition, we aimed to assess the effects of anthropogenic features commonly found across the lesser prairie-chicken's distribution, including oil wells, towers and windmills, powerlines, roads, and fences, during these movements. We also tested whether there were regional differences in response that should be accounted for in landscape-scale connectivity models. Results from this study will provide a better understanding of landscape selection during the long-distance movements that are likely crucial for population persistence in this spatially distributed species. Parameter estimates will also allow for the creation of a connectivity model using least-cost path or similar methods to better identify connectivity zones among leks for lesser prairie-chicken conservation.

Methods

We used GPS location data from lesser prairie-chickens collected from multiple sites across the geographic distribution from March 2013 – December 2016. Sites included east-central New Mexico (Chaves, Lea, and Roosevelt Counties), southeast Colorado (Cheyenne, Prowers, and Baca Counties), the Oklahoma panhandle (Beaver County), and two separate study regions from Kansas: the south-central region (Clark, Kiowa, and Comanche Counties) and the northwest region (Gove and Logan Counties). Some birds from the New Mexico and Oklahoma study regions crossed into Texas, and the Colorado study region also had two birds that made long-

distance movements in southwest Kansas. These five regions were defined separately as there was variation in the natural landcover (McDonald et al. 2014) and feature densities (Chapter 1) among most regions. Similar capture techniques were used across all study regions: lek-focused dropnets (Silvy et al. 1990) and walk-in drift traps (Haukos et al. 1990; Schroeder & Braun 1993). Rump-mounted GPS transmitters (22 g PTT- 100, Microwave Telemetry Inc., Columbia, Maryland, USA; Model 22GPS, North Star Science and Technology, King George, Virginia, USA) were fitted to each individual bird (n = 346). Long-distance movements were then delineated from the overall dataset following methods in Earl et al. (2016), where any consecutive group of points (i.e., burst) found greater than 5 km net displacement outside the individuals home range (i.e., 95% kernel density estimation) was classified as a long-distance movement.

Landcover and Feature Variables

As part of this study, we sought to test which landcover types lesser prairie-chickens use during long-distance movements. To accomplish this, we used the 2011 National Land Cover Database (NLCD) raster (Homer et al. 2015) for our study region. We also wanted to assess the selection response to CRP. To do this, we obtained CRP polygon data from the Southern Great Plains Crucial Habitats Assessment Tool (hereafter 'CHAT'; Klute et al. 2013), which had anthropogenic feature and CRP data for the geographic distribution of lesser prairie-chickens around the same time our study period started. Using ESRI ArcGIS 10.3 (ESRI 2014), we reclassified the NLCD raster into four categories. The cropland and hay/pasture categories were the same as their respective original NLCD classifications, while our natural landcover category was composed of the Shrub/Scrub, Grassland/Herbaceous, and Barren NLCD classifications. The last category, Other, was made of the remaining landcover classification in our study region including open water, wetlands, human developed landcovers, and forests. We then overlaid the CRP layer on the NLCD raster, adding a fifth and final category to create our landcover raster. Our CRP data was incomplete in some areas with long-distance movements in the New Mexico

study region. To deal with this, we removed the movements that occurred outside our CRP data boundary from our analysis. In addition to landcover, we also included elevation as an environmental variable using a digital elevation map (DEM) from USGS.

Data for anthropogenic features was obtained to test the response to these structures during long-distance movements. Road data was collected from the U.S. Census Bureau 2016 TIGER/Line dataset for our study area. While the average use of particular roadways may impact response trends, we were unable to find traffic data across our entire study area and therefore included both highways and rural roads in this feature category. We also wanted to test the effects of large powerlines (i.e., powerlines that carry over 69 kV of electricity). This data was readily available nationwide from the U.S. Department of Homeland Security and represents tall linear features in the landscape that carry electricity long distances. Data for smaller powerlines (i.e., residential powerlines) was only available for the Oklahoma study region, so we were unable to include these structures in our analysis. Data for large structures greater than 50 ft tall (i.e., poles, towers, buildings, windmills, stacks, utilities) was obtained from the Federal Aviation Administration's Digital Obstacle File and were considered in analysis together as towers. Oil well data was gathered from the CHAT dataset and included active oil and gas well locations from 2010 to 2013 across our study area. This dataset was incomplete in the Colorado region, so we ended up removing most long-distance movements in that study region from our analysis. While inactive wells could also impact movements, we were unable to find reliable well data across our entire study region detailing when pumps were active vs inactive, so we used this dataset for consistency. We also wanted to assess the response to fences. Fence data was delineated and ground-truthed using ArcGIS at both the Kansas study regions (Robinson et al. 2016) and in the Oklahoma region. However, this data was focused around lek sites and did not cover all long-distance movement tracts in these regions.

Resource Selection Functions

We used discrete choice models to evaluate resource selection during long-distance movements. This allowed us to stratify our analysis by individual movements and match available points to the area available during that movement (McDonald et al. 2006). Conditional logistic regression using the package 'survival' in R (*version 3.4.2*, R Core Team 2017) was used to conduct all analyses. We used each long-distance movement path as our strata, where we matched the known used GPS relocation points along each movement path with available points from the surrounding area. This allowed for the movement paths to be the sample unit and assumes that selection decisions were being made at similar scales to the movement itself. To do this, each long-distance movement tract was buffered by the mean step distance (2.7 km), and this area was used to draw the available locations randomly and matched to each movement. As suggested by Northrup et al. (2013), we tested models with varied available sample sizes ranging from 10-10,000 available points per movement to ensure variable estimate convergence and observed convergence of all estimates at sample sizes greater than 3,000.

Explanatory variables were then extracted to each used and available point. This included landcover type, elevation, and data for anthropogenic features. For the landcover variable, the 'Natural Landcover' type was used as the reference category in all models. Elevation was scaled by its mean for analysis. For each of the anthropogenic structures, we created three density rasters with different radii using results from a recent study that assessed the distance at which lesser prairie-chickens responded to these features during long-distance movements (Table 1; Chapter 1). This was done to examine what scale had the strongest relationship with selection during long-distance movements for each variable. We also calculated the distance to the nearest feature for each anthropogenic structure at every point, which was log-transformed for analysis. Pearson correlation coefficients between the different rasters and distance to nearest structure indicated correlation (> 0.60) among the different metrics (i.e., nearest feature and density estimates) for each feature type so only one variable per feature was included in RSF analyses.

Similar to Elliot et al. (2014), RSF's were conducted in two steps. First, we assessed univariate models for the anthropogenic structures to determine the effect different structure distribution metrics have on selection. For each structure, this included the three density rasters that estimated the feature density across different scales, as well as the variable created that calculated the distance to the nearest structure from each point in our analysis. We used model ranking to identify the top performing variable for each feature type based on Akaike Information Criterion (AIC; Burnham & Anderson 2003). The univariate model for each structure type with the lowest AIC ranking (i.e. most parsimonious) was used in RSF analyses in the next step. In other words, the chosen variable for each feature was assumed to be the metric at which lesser prairie-chickens selected for during long-distance movements. Second, we developed a set of models representing six competing hypotheses about whether landcover, anthropogenic features, or both best predicted lesser prairie-chicken selection during long-distance movements (Table 2). Models included a full model with all environmental and anthropogenic explanatory variables and three models testing varying hypotheses of the effects of anthropogenic features. These consisted of a model representing linear features in the landscape, one comprised of all vertical features, and one representing the tallest features in the landscape (i.e., large powerlines and towers). In addition, we included a landcover model with only cover type and elevation as explanatory variables and an elevation-only model that served as a single parameter null model.

In the main analysis, we wanted to examine population-wide estimates and compare regional differences. Adding interactions for study regions with each explanatory variable, as these variables all showed some variation by region (Chapter 1), would have resulted in an overly complicated model. To address this, we completed both the above steps (univariate feature analysis and alternative model selection) three times. The first being an analysis with all the study regions together to obtain population-wide estimates. In the second part, we split data up into study regions and completed the RSF analysis in each region. This allowed us to compare regions for overlap in estimates without overcomplicating the models with regional interactions.

However, we removed the Colorado and New Mexico data as we ran into model convergence errors stemming from the limited data in these regions. We completed alternative model selection for each of the remaining regions in Kansas and Oklahoma. The third analysis was similar to the regional analysis, but we subsetted the data even further so we could evaluate potential selection in relation to fences. We only had fence data for select areas in the three study regions from the previous analysis. Due to this, fences were not included as an explanatory variable in the first two parts of the main RSF analysis. Our data was clipped to the areas where fences were mapped and fence-focused regional RSF analyses were completed for this subsetted data including fence features in the alternative models. We included this analysis because the impact of fences on lesser prairie-chickens is mixed (Wolfe et al. 2007; Robinson et al. 2016). As the probability of encountering fences increases greatly during long-distance movements, it is important to estimate if birds respond to these structures during movements.

Results

We initially had GPS data for 346 lesser prairie-chickens across their complete geographic distribution. Of these, 77 lesser prairie-chickens made long-distance movements in our study area. This consisted of 4,331 total GPS locations and 158 long-distance movements for the population-wide analysis (Table 3). We further reduced our sample size to 3,893 and 1,643 total locations for the region and fence-focused analyses respectively. Lesser prairie-chickens making long-distance movements were most common in the Kansas study regions where we had the highest number of individuals with GPS units. At least two lesser prairie-chickens in each study region made >1 long-distance movement for a total of 34 birds.

Landcover varied by region (Table 4). The natural landcover classification was the most common landcover type with over 60% coverage among all regions (Table 4). Cropland was most abundant in the Kansas northwest and Colorado regions. CRP covered almost 17% of the land in the Colorado region, while it consisted of less than 7% in the other study regions. The least

common cover type was hay/pasture. It consisted of less than 3% of the total available area in all regions and was not found in the New Mexico region at all. In addition, there was variation in anthropogenic structure density among study regions (Table 4). Oklahoma had the highest density for all feature types measured except for oil wells where Colorado had the highest density. Besides Oklahoma, the Kansas regions had the highest densities of large powerlines. Fence density was similar among the Kansas regions but was estimated almost 3 km per 2 km^2 greater in Oklahoma (Table 4). Towers tended to be the least common feature found across our study areas. The Oklahoma region, followed by the Kansas south-central region, had the greatest tower densities. Roads had the highest density in the Oklahoma and Colorado regions, while the Kansas regions had the lowest.

Univariate analyses for anthropogenic feature variable type yielded similar results in all three parts of our study (Appendix A). Only tower features in the regional univariate tests revealed a competitive model (< 2 dAIC; Table A2), but we chose to use the most supported metric variable for each feature type. The top variable for each feature was the same among all analyses. For large powerlines, the univariate response was best modeled by the distance to the nearest feature. In contrast, all but one of the other features were best modeled by the features respective density using the maximum response distance identified in Chapter 1 (i.e., medium density; Table 1). This was 400 m, 700 m, and 11250 m for oil wells, roads, and towers respectively. The only exception was seen with fences, where univariate models indicated that the most supported metric was 1.5 times the maximum observed response distance from Chapter 1 at 600 m.

For the population-wide analysis of dispersal, we identified the full model containing landcover type, elevation, and all the anthropogenic features from the univariate analysis as the most supported model (Table B1). This suggests that lesser prairie-chickens respond to all the landscape variables we tested during long-distance movements. All variables tested had either significantly positive or negative estimates at the 95% confidence interval indicating strong

selection or avoidance behaviors on the population-wide scale (Table 5). For landcover, hay/pasture and CRP were selected for in comparison to our natural landcover reference category, while cropland and the 'other' cover type were avoided. Lesser prairie-chickens avoided all anthropogenic features. Lesser prairie-chickens selected for areas at greater distances from large powerlines. For the other structures estimated with density metrics, lesser prairie-chickens selected for areas with lower densities of structures. Tower density had the strongest avoidance response followed by oil well density (Table 5). In addition, higher elevations tended to be selected for during long-distance movements.

For analyses examining differences among regions, the full model containing all landscape variables tested was also the best fit for the data (Appendix Table B2). We had no bird locations in the Kansas south-central region in the Hay/Pasture cover type (< 0.03 % regional cover; Table 4), which led us to drop that variable from all our models in that region. CRP was significantly selected for in the Oklahoma region while Cropland was significantly avoided in all regions in comparison to Natural Landcover (Table 6). Results also indicated that birds selected for higher elevations during long-distance movements regardless of the study region. Oil wells were the only feature to have consistently significant avoidance trends among all regions. For all of the other anthropogenic features tested, while there was regional variation with significance, model estimates indicated avoidance trends as well.

For the fence-focused regional analysis, we had to remove the Hay/Pasture cover type from the Oklahoma study region in addition to the Kansas south-central, because no birds used this relatively rare cover type (< 0.2 % regional coverage; Table 4). The full model containing all variables was ranked as the most parsimonious model by AIC among all regions (Table B3). Prairie-chickens from both the Kansas regions avoided fences. In comparison, lesser prairie-chickens in Oklahoma did not avoid fences. There was also variation in significance for many estimates when comparing the fence-focused regional models to the regional models (Table 7). However, this was most likely because this analysis used only a subset of the data in the analysis,

as it was the same regions as the regional analysis clipped to the areas we had fence data and was not representative of the entire region as a whole.

Discussion

Long-distance movements ensure connectivity and help drive population-wide processes, such as gene flow and the rescue of declining populations (Hanski 1999; Clobert et al. 2001; Hedrick 2011). Long-distance movements can be influenced by features in the landscape and lead to differential selection of habitat (Wilson et al. 2012; Abrahms et al. 2016a). Conservation corridors work to mitigate the effects of fragmentation and maintain parts of the landscape that link spatially distributed populations together (Bennett 2003). In our study, we found that landcover, anthropogenic features, and elevation are important during long-distance movements of lesser prairie-chickens. As such, all of these factors should be considered when designating corridors to manage for population connectivity.

While managing for continuous tracts of habitat may be preferable, in a heavily altered landscape connectivity may be accomplished through the management of smaller stepping stones (i.e., smaller patches that provide areas to rest or forage during dispersal movements; Söndgerath & Schröder 2002; Saura et al. 2014) or strips of land with lower anthropogenic disturbance than other portions of the landscape. Our results indicated that lesser prairie-chickens select for CRP and hay/pasture landcovers in contrast to overall availability during long-distance movements in our population-wide model (Tables 4 and 5). This suggests that these landcover types may provide good stopovers as lesser prairie-chickens make these connective movements. The presence of stepping stones has been reported to assist dispersals in other species (Conradt et al. 2001; Herrera et al. 2017; Luja et al. 2017).

The effectiveness of corridors and stepping stones at aiding long-distance movements may be influenced by the permeability of the matrix as a whole (Baum et al. 2004). This makes it necessary to identify landcovers and other landscape features that may negatively impact

connectivity. In comparison to other cover types, we found that cropland and the 'other' category were the least suitable for lesser prairie-chickens during long-distance movements with cropland being significantly avoided in all analyses. In addition, we found that the birds selected for areas with lower densities of towers, oil wells, roads, and fences, as well as areas that were furthest from the nearest large powerlines in the landscape (Tables 5- 7). Avoidance response to anthropogenic features has been observed in other grouse species during different life cycle periods (Hovick et al. 2014; Winder et al. 2015b), other grassland birds (Thompson et al. 2015), and in mammal species (Laberee et al. 2014; Northrup et al. 2015). Furthermore, in all regional models and the population-wide model, the tower variable consistently had strong relative negative effect on long-distance movements. This coincides with evidence that taller features, such as powerlines and windmills, are avoided at larger distances and crossed less than roadways by lesser prairie-chickens (Pruett et al. 2009; Hagen et al. 2011; Chapter 1), but this is not seen in all grouse species (Harrison et al. 2017; LeBeau et al. 2017). Avoidance of oil wells was also significantly negative among all regional and population model estimates. In other grouse populations, oil and gas development had the largest negative effect on populations (Hovick et al. 2014), but this could be due to the density that these features are typically constructed in or their distance to critical habitat areas (i.e., lek sites). Understanding responses to these features during long-distance movements will help in the identification of accurate corridors in the landscape and prevent barriers to movement (Abrahms et al. 2016b; Benz et al. 2016).

While our approach allowed us to identify similar directional trends in both population-wide and regional analysis for the selection on the landscape during long-distance movements, it did have its limitations. In our regional analysis, we could only compare relative trends in the response magnitude, because selection in different regions were estimated using different available areas. However, our analysis did allow us to conclude that there were no significant differences in selection direction among regions for any variables tested. In other words, response estimates for the CRP and hay/pasture landcover variables were either positive (i.e., indicating

selection for the landcover compared to our reference category) or nonsignificant, while responses to cropland, the 'other' landcover type, and anthropogenic features either indicated avoidance or were nonsignificant. These trends in directional response to anthropogenic features are similar to meta-analyses of these impacts on grouse species in general (Hagen 2011; Hovick et al. 2014).

In addition, our univariate method makes a direct comparison of magnitude for the anthropogenic features difficult, because the densities were measured at different scales (i.e., different radii distances) for each feature. There is a tradeoff between considering scales that may be more biologically relevant for response to specific features during long-distance movements of lesser prairie-chickens and choosing a uniform scale for all features. Allowing the univariate selection to identify the most important scales for response to particular features, in addition to using quantitatively derived response distances (Table 1) as the basis for the density radii, we identified the functional scale that these features affected long-distance movements. Choosing one response scale for all features, while making the models easier to interpret, is likely to have less biological relevance if response distance is highly variable among feature types. Response to landscape features has been shown to be behavior-dependent (Wilson et al. 2012; Abrahms et al. 2016a), and there is evidence that lesser prairie-chickens respond to taller landscape features at greater distances during long-distance movements (Chapter 1). Thus, we accepted the method with less direct interpretability but more biological relevance when using our estimates to model connectivity corridors for the species.

Research often focuses on localized population dynamics (e.g., home ranges, breeding or nesting grounds; Barten et al. 2001; Doherty et al. 2008; Dinkins et al. 2014). This can be important as these areas are generally where the life cycles of individuals are centered and directly support the individuals in the local area (Winder et al. 2015a). However, if movement and connectivity at larger scales are not considered in management, continued fragmentation may reduce the probability of population persistence (Fuhlendorf et al. 2017). We expect that

management for natural landcover, CRP, and hay/pasture in connective pathways would be beneficial to lesser prairie-chickens during long-distance movements. We found that lesser prairie-chickens preferentially selected for the CRP and hay/pasture cover types during long-distance movements in our population-wide model. While there is discussion that monoculture dominant hay/pasture landcover may cause sink habitats for grouse species (Rodgers & Hoffman 2005; Davis et al. 2008), it may be suitable for use as a stopover during long-distance movements, but further analysis to estimate fitness during these movements is needed to draw further conclusions. It may also be important to consider that our analysis may have classified previously enrolled CRP land that has been left as pasture into this category as well (USDA-NRCS 2015; Morefield et al. 2016).

In addition, connectivity in the landscape may also be affected by an individual's avoidance response to discrete features in the landscape. We observed avoidance responses to all anthropogenic features during long-distance movements. The greatest avoidance response was for tower features in all regions, despite their relatively low densities. Lesser prairie-chickens were identified to have the largest response distance to towers as well (Chapter 1), providing further support for the negative effects these features could have on long-distance movements. However, oil wells were the only feature to have a significant effect in all population-wide and regional analyses. Oil wells were observed to have an effect on the negative displacement of grouse in a meta-analysis (Hovick et al. 2014). As all of these features can have negative effects on the long-distance movement of grouse, we recommend mitigation efforts for the construction of new features in important pathways using the response distances identified as important for selection through our univariate analysis as buffer distances for these features in movement corridors.

We also observed selection for higher relative elevation across all regions and the population-wide analyses. While higher elevation has been identified as an important landscape characteristic in lek site selection of grouse (Gregory et al. 2011; Hovick et al. 2015), it was not a significant factor in resource utilization within home ranges of greater prairie-chickens (Winder et al. 2014).

Our results show that ridges and hilltops are used during long-distance movements. Higher relative elevation could be used to help survey the surrounding environment for a suitable location to settle or to allow higher vigilance for predators in unfamiliar territories. It may be important to prioritize management for land at higher relative elevation when maintaining movement corridors.

Corridors and landscape-scale management may provide the best solution to conserving connectivity and long-term population persistence for lesser prairie-chickens in the Southern Great Plains (Franklin 1993; Fuhlendorf et al. 2017). Our study indicates that during long-distance movements, lesser prairie-chickens tend to avoid all types of anthropogenic features across the landscape, with tower density having the greatest effect. We also found that landcover type affects bird paths, with birds selecting for a mixture of CRP, hay/pasture, and natural landcovers over cropland during these movements. This implies that converting cropland to grassland could help provide stepping stones through areas with higher densities of cropland. Our results emphasize that management of both landcover and human development are important to maintaining connectivity among lesser prairie-chicken populations. As we observed no directional response changes in regional analyses, we believe using population-wide estimates would provide a conservative measure to build connectivity models. These estimates will be useful in creating a map of potential corridors between lek sites and outlining connectivity zones. Ultimately, results from this study will assist in the identification of areas of concern that should be protected from further development, avoid the creation of barriers to dispersal, and maintain gene flow in the metapopulation.

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Tables

Table 1

The distances used to create the density rasters at different scales for the univariate anthropogenic feature selection. The middle scale for each feature was the maximum response distance to that feature observed in Chapter 1, using the same data as this analysis. The other two scales are 0.5 and 1.5 times the observed maximum response.

Anthropogenic Feature	Density Radius (m)
Towers	5625, 11250, 16875
Oil Wells	200, 400, 600
Large Powerlines	4975, 9950, 14925
Roads	350, 700, 1050
Fences	200, 400, 600

Table 2

Alternative models tested using the results from univariate analysis to select the variables used for each anthropogenic structure.

Model	Description
Full	cover type + elevation + large powerlines + oil wells + roads + towers + (fences[1])
Vertical Features	large powerlines + oil wells + towers
Linear Features	large powerlines + roads + (fences[1])
Tall Features	large powerlines + towers
Landcover	cover type + elevation
Elevation Only	elevation

[1]The fence feature type was only added in the fence-focused regional model.

Table 3

Distribution of long-distance movements and the number of birds making these movements across the five study regions.

	Population-wide Dataset		Fence Model Dataset	
Region	**Birds**	**Long-distance Movements**	**Birds**	**Long-distance Movements**
Colorado	2	13	-[1]	-
Kansas	25	38	19	30
Northwest Kansas	33	60	29	42
Southcentral New Mexico	4	17	-	-
Oklahoma	13	30	5	8
Total	77	158	53	80

[1] indicates study regions without fence data.

Table 4

Regional comparisons in landcover percentages and anthropogenic structure density in 2 km^2 grid cells [mean ± SE].

		Region				
	Variable	Colorado	Kansas Northwest	Kansas Southcentral	New Mexico	Oklahoma
Percent Landcover	Crop	13.0182	16.9677	5.3111	1.9158	5.5404
	CRP	16.9554	5.4836	3.9301	4.8596	6.7265
	Hay/Pasture	0.0046	2.2474	0.0258	-[3]	0.1417
	Natural Landcover	62.3431	70.1907	85.0196	91.4724	80.9326
	Other	7.6787	5.1106	5.7134	1.7522	6.6588
Feature Density[4]	Towers[1]	0.0552 ± 0.0233	0.0583 ± 0.0118	0.1101 ± 0.0164	0.0195 ± 0.0048	0.1608 ± 0.0206
	Large Powerlines[2]	92.9015 ± 14.2568	151.1092 ± 9.65	128.5422 ± 9.3843	79.8298 ± 10.3072	217.6607 ± 18.029
	Oil Well[1]	2.6699 ± 0.0844	0.5576 ± 0.0213	0.9006 ± 0.0296	1.4325 ± 0.1034	1.9435 ± 0.0411
	Road[2]	5535.5444 ± 146.2134	4097.0933 ± 59.46	4340.2507 ± 58.6791	4987.5379 ± 93.4855	5653.3854 ± 74.3937
	Fence[2]	-	5394.4502 ± 190.0596	5273.2055 ± 188.5491	-	8206.5172 ± 706.3542

[1] These structures were estimated as the average count per 2 km^2.
[2] These structures were estimated as the average length (m) per 2 km^2.
[3] 'Dashes' indicate areas removed from analysis due to missing data in the study area.
[4] Feature density was estimated using the same methods as Chapter 1.

Table 5

Beta estimates (SE) for selection during long-distance movements of lesser prairie-chickens obtained from top model of the discrete choice analysis using population-wide data.

Explanatory Variables	Population-wide Model
CRP	0.3437 (0.0484) *
Hay / Pasture	0.3575 (0.1397) *
Crop	-0.3755 (0.0481) *
Other	-0.3275 (0.1074) *
Elevation	1.653 (0.1775) *
Large Powerlines Near Distance	0.1329 (0.0248) *
Oil Density 400 m	-0.2163 (0.0265) *
Road Density 700 m	-0.2007 (0.0191) *
Tower Density 11250 m	-4.3892 (0.7372) *

* indicates the parameter estimate confidence intervals did not overlap 0 at the 95% level.

Table 6

Beta estimates (SE) for selection during long-distance movements of lesser prairie-chickens obtained from top models of the regional discrete choice analysis.

Explanatory Variables	Kansas Northwest	Kansas South-central	Oklahoma
CRP	0.1202 (0.0967)	-0.1196 (0.116)	0.4777 (0.0763) *
Hay / Pasture	0.2669 (0.1517)	-[1]	0.7575 (0.3877)
Crop	-0.4835 (0.0752) *	-0.3321 (0.0875) *	-0.3368 (0.0969) *
Other	-0.1765 (0.2141)	-0.6051 (0.1777) *	-0.1664 (0.1824)
Elevation	0.9196 (0.307) *	1.3746 (0.3071) *	5.0462 (0.4222) *
Large Powerlines Near Distance	0.0808 (0.0529)	0.0552 (0.0379)	0.1912 (0.0447) *
Oil Density 400 m	-0.2684 (0.0643) *	-0.2079 (0.0501) *	-0.1863 (0.0393) *
Road Density 700 m	-0.2329 (0.0463) *	0.0428 (0.0317)	-0.3721 (0.0299) *
Tower Density 11250 m	-3.709 (5.2018)	-6.7369 (1.2936) *	-4.3261 (0.876) *

* indicates the parameter estimate confidence intervals did not overlap 0 at the 95% level.

[1] 'dash' indicates parameter not included in the model.

Table 7

Beta estimates (SE) for selection during long-distance movements of lesser prairie-chickens obtained from top models of the fence-focused regional discrete choice analysis.

Explanatory Variables	Kansas Northwest	Kansas South-central	Oklahoma
CRP	-0.5244 (0.1529) *	-0.4335 (0.2288)	0.0369 (0.1865)
Hay / Pasture	0.3704 (0.1768) *	-[1]	-
Crop	-0.315 (0.1094) *	-2.7499 (0.5805) *	-0.8212 (0.2859) *
Other	-0.2823 (0.3594)	-0.6596 (0.2539) *	0.517 (0.4265)
Elevation	-0.4263 (0.563)	4.559 (0.5855) *	2.5659 (1.1151) *
Large Powerlines Near Distance	0.0485 (0.079)	0.116 (0.0696)	-0.2986 (0.2528)
Oil Density 400 m	-0.3672 (0.1003) *	-0.1676 (0.0677) *	-0.0666 (0.0713)
Road Density 700 m	-0.4502 (0.0742) *	0.0511 (0.0462)	-0.7233 (0.095) *
Tower Density 11250 m	-7.8851 (25.8336)	11.2397 (14.4863)	-685.6824 (127.8348) *
Fence Density 600 m	-0.2107 (0.0461) *	-0.2439 (0.0333) *	-0.0923 (0.083)

* indicates the parameter estimate confidence intervals did not overlap 0 at the 95% level.

[1] 'dashes' indicate parameters not included in the model.

Appendix A

Results from univariate analysis of anthropogenic features for each of the three datasets. The top variable for each feature type was used in alternative RSF models.

Table A1

Population-wide univariate analysis results indicating what variables were used in the alternative RSF models.

Feature Type	Variable	ΔAIC	K	Weight	β	SE(β)
Large Powerlines	Near Distance	0.00	1	0.998	0.1722	0.0252
	Density 4975 m	12.62	1	0.002	-1.4400	0.2365
	Density 9950 m	22.86	1	0.000	-2.4731	0.4598
	Density 14925 m	45.19	1	0.000	-2.3732	0.9271
Towers	Density 11250 m	0.00	1	0.976	-3.4023	0.6758
	Near Distance	7.65	1	0.021	-0.1407	0.0295
	Density 16875 m	11.81	1	0.003	-3.2223	0.7832
	Density 5625 m	25.56	1	0.000	-0.8789	0.4608
Oil Wells	Density 400 m	0.00	1	1.000	-0.2306	0.0265
	Density 200 m	16.35	1	0.000	-0.1278	0.0179
	Near Distance	36.37	1	0.000	0.1613	0.0221
	Density 600 m	56.49	1	0.000	-0.1818	0.0320
Roads	Density 700 m	0.00	1	1.000	-0.2220	0.0188
	Density 350 m	56.82	1	0.000	-0.1074	0.0117
	Density 1050 m	96.98	1	0.000	-0.1708	0.0246
	Near Distance	123.68	1	0.000	0.0646	0.0138

Table A2

Regional Dataset

Regional univariate analysis results indicating what variables were used in the alternative RSF models. This dataset included all movements in the Oklahoma and both Kansas study regions.

Feature Type	Variable	ΔAIC	K	Weight	β	SE(β)
Large Powerlines	Near Distance	0.00	1	0.958	0.1609	0.0251
	Density 4975 m	6.27	1	0.042	-1.4341	0.2365
	Density 9950 m	18.73	1	0.000	-2.3657	0.4605
	Density 14925 m	41.24	1	0.000	-1.8351	0.9365
Towers	Density 11250 m	0.00	1	0.699	-0.1698	0.0296
	Near Distance	1.70	1	0.299	-3.4439	0.6845
	Density 16875 m	11.68	1	0.002	-3.4143	0.7899
	Density 5625 m	28.36	1	0.000	-0.7561	0.4551
Oil Wells	Density 400 m	0.00	1	0.995	-0.2312	0.0278
	Density 200 m	10.66	1	0.005	-0.1347	0.0194
	Near Distance	40.53	1	0.000	0.1491	0.0230
	Density 600 m	55.71	1	0.000	-0.1683	0.0329
Roads	Density 700 m	0.00	1	1.000	-0.2169	0.0196
	Density 350 m	53.97	1	0.000	-0.1011	0.0121
	Density 1050 m	87.93	1	0.000	-0.1619	0.0259
	Near Distance	113.17	1	0.000	0.0545	0.0145

Table A3

Fence-focused regional univariate analysis results indicating what variables were used in the alternative RSF models. This dataset included movements in the Oklahoma and both Kansas study regions that were clipped to areas that overlapped fence data.

Feature Type	Variable	ΔAIC	K	Weight	β	SE(β)
Large Powerlines	Near Distance	0.00	1	0.732	10.7077	2.3933
	Density 14925 m	2.76	1	0.184	0.1988	0.0497
	Density 4975 m	4.35	1	0.083	-1.6774	0.4294
	Density 9950 m	20.33	1	0.000	0.0486	0.8607
Towers	Density 11250 m	0.00	1	0.493	-26.9536	12.5297
	Near Distance	0.36	1	0.412	-0.1442	0.0670
	Density 16875 m	4.68	1	0.048	2.0914	4.9857
	Density 5625 m	4.70	1	0.047	-3.6182	9.2078
Oil Wells	Density 400 m	0.00	1	0.999	-0.2109	0.0432
	Density 200 m	14.12	1	0.001	-0.0843	0.0251
	Near Distance	22.93	1	0.000	0.0835	0.0351
	Density 600 m	27.03	1	0.000	-0.0598	0.0471
Roads	Density 700 m	0.00	1	1.000	-0.3304	0.0345
	Density 1050 m	26.64	1	0.000	-0.3707	0.0450
	Density 350 m	60.30	1	0.000	-0.1261	0.0219
	Near Distance	91.28	1	0.000	0.0450	0.0218
Fence	Density 600 m	0.00	1	1.000	-0.2522	0.0240
	Density 400 m	25.75	1	0.000	-0.1781	0.0191
	Density 200 m	69.16	1	0.000	-0.0861	0.0128
	Near Distance	89.42	1	0.000	0.1124	0.0216

Appendix B

Results from analysis competing model hypotheses for each of the three datasets.

Table B1

Model selection using AIC for the population-wide data.

Model	ΔAIC	K	Weight
Full	0.00	9	1.0000
Landcover	280.02	5	0.0000
Linear Features	333.14	2	0.0000
Vertical Features	355.80	3	0.0000
Tall Features	445.34	2	0.0000
Elevation Only	478.04	1	0.0000

Table B2

Model selection using AIC for the regional data.

	Kansas Northwest			Kansas South-central			Oklahoma		
Model	**ΔAIC**	**K**	**Weight**	**ΔAIC**	**K**	**Weight**	**ΔAIC**	**K**	**Weight**
Full	0.00	9	1.0000	0.00	8	1.0000	0.00	9	1.0000
Landcover	47.22	5	0.0000	47.86	4	0.0000	257.39	5	0.0000
Linear Features	67.68	2	0.0000	73.38	2	0.0000	270.44	2	0.0000
Vertical Features	85.90	3	0.0000	36.48	3	0.0000	371.32	3	0.0000
Tall Features	106.55	2	0.0000	56.62	2	0.0000	408.74	2	0.0000
Elevation Only	112.25	1	0.0000	69.43	1	0.0000	340.67	1	0.0000

Table B3

Model selection using AIC for the fence-focused regional data.

	Kansas Northwest			Kansas South-central			Oklahoma		
Model	**ΔAIC**	**K**	**Weight**	**ΔAIC**	**K**	**Weight**	**ΔAIC**	**K**	**Weight**
Full	0.00	10	1.0000	0.00	9	1.0000	0.00	9	1.0000
Linear Features	33.07	3	0.0000	128.84	3	0.0000	70.08	3	0.0000
Landcover	81.30	5	0.0000	56.78	4	0.0000	207.33	4	0.0000
Vertical Features	81.39	3	0.0000	183.14	3	0.0000	126.62	3	0.0000
Elevation Only	101.77	1	0.0000	148.35	1	0.0000	217.45	1	0.0000
Tall Features	103.83	2	0.0000	188.14	2	0.0000	130.69	2	0.0000

VITA

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